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RESPIRATION OF DORMANT SEEDS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 282

HOPE SHERMAN

(WITH FOUR FIGURES)

Introduction

Plant physiologists have long been interested in the physiological processes associated with the development and particularly with the germination of seeds. Much attention has been devoted to those seeds which, when ripe, fail to respond to germinating conditions unless subjected to special treatment or permitted to undergo a distinct rest period. Such dormant seeds offer many problems to pique the curiosity of the investigator, and work on individual seeds has given some conception of the environmental factors influencing dormancy (4, 15, 17, 40), as well as of the internal conditions retarding germination and of the chemical changes which take place in after-ripening (19, 25, 27, 38). Furthermore, dormant seeds often retain their viability for long periods of time. BEALE (7, 8, 24, 41) reported that *Amaranthus retroflexus* will remain viable in the ground for thirty years. If such seeds are fully imbibed, their remarkably prolonged viability may be due either to especially large food reserves or to a tremendous reduction of the rate at which such reserves are respired. A study of the respiration of stored seeds at different time intervals might help to interpret this point.

While the respiration of most plant parts has been studied more or less, there are comparatively few data on resting seeds. For this reason the study of the respiration of seeds would be of interest, per se, and if dormant seeds were selected, it might be possible both to discover differences in the respiration of related and of unrelated species, and, through the acquisition of information upon the rapidity with which food reserves were utilized, to arrive at some idea of the probable longevity of the seeds.

Most dormant seeds belong to one or another of certain main classes (CROCKER 14): those in which the dormancy is due to coat characters, as impermeability to water or to oxygen, acting in conjunction with some physiological character in the embryo aside from actual dormancy; or those in which dormancy is conditioned by the embryo itself, either through lack of differentiation or through the absence of some factor essential for germination, even when the naked embryo is exposed to all ordinary external germination conditions. In addition there are certain seeds with mature embryos whose coats apparently exclude neither water nor oxygen, but still germination is hindered; such delay in *Alisma Plantago* (15) is due to the inability of the embryo to overcome the mechanical resistance to expansion offered by the coats. Finally, dormancy may result from the joint action of two or more of these factors.

In the investigation, some of the results of which are embodied in this paper, the original intention was to study the respiration of each type of dormant seeds, but during the progress of the work the comparative respiration of dormant seeds has become of prime interest, and this phase forms the subject of the present report.

The seeds selected were three on which physiological studies had already been made, but for which respiratory data were lacking, namely, *Amaranthus retroflexus*, *Chenopodium album*, and *Crataegus*,¹ and in addition (because of their economic importance and the ease with which they could be obtained, as well as because of their relationship to *Crataegus*) seeds of the common drupaceous Rosaceae. In *Crataegus* and *Amaranthus* some attempt has been made to determine variations in respiration accompanying after-

¹ The species chiefly studied was *C. coccinea*.

ripening or aging. Furthermore, since many workers claim that catalase activity varies with the respiration, catalase determinations have been made on most of the seeds used.

Methods

Catalase activity was measured by the volume of oxygen set free from hydrogen peroxide (the Oakland Chemical Company's dioxogen) by a given weight of seeds. The apparatus was essentially that described by APPLEMAN (1), and the routine procedure was to grind the seeds for one minute in a mortar with sand and calcium carbonate, add 5 cc. of distilled water, and grind a second minute. The contents of the mortar were then transferred to a bottle which was placed in a water bath at 25° C. The level of the gas burette was adjusted, and after sufficient time had elapsed for the seed suspension to come to the temperature of the bath, the exit of the gas burette was closed. Constancy of level of the water meniscus in the gas burette was assumed to indicate stability of temperature. Thereupon the cock of the dropping funnel was opened on the minute, and 5 cc. of dioxogen was allowed to flow into the bottle, which was immediately set shaking. Readings of the volume of oxygen liberated were taken on the gas burette every minute for the first five minutes and on the tenth minute also.

The respiration determinations were made by means of a respirometer designed by CROCKER (26). This consists of a cylindrical glass chamber fitted with a glass stopper through which pass two tubes, one a manometer and the other a short, straight tube provided with a stopcock by which the chamber can be closed to the surrounding air. Seeds which had been soaked for twenty-four hours and thereafter stored on moist filter paper at about 10° C. were placed in a porcelain hooded holder, designed by HARRINGTON (25). This holder was supported within the respirometer on projections from its wall about 1 cm. above the base. The respirometer was placed in a water bath at constant temperature, and after half an hour the mercury in the manometer was brought to a level and the stopcock closed. When the experiment was to be brought to an end, the difference between the mercury levels in the two arms of the manometer was measured, and a known volume of caustic potash was introduced into the

respirometer through the stopcock tube. The potassium hydroxide was allowed to flow down the sides of the respirometer, the hood of the seed holder preventing its coming into contact with the seeds. So far as possible, measurements were made and absorption carried out without removing the respirometer from the bath. A second reading of the manometer was taken after absorption of the carbon dioxide. Barometer readings were taken after closing the chamber at the beginning, and again before absorption of the carbon dioxide at the end of the experiment. From the calibration of the respirometer it was possible to calculate its volume at the beginning (corrected for the volume occupied by the seeds) and at the end, before and after carbon dioxide absorption, a correction for the volume of the absorbent added being applied in the latter case. All volumes were further corrected to absolute zero, and to 760 mm. pressure. The difference between the volumes at the end of the experiment before and after carbon dioxide absorption represents the volume of carbon dioxide eliminated by the seeds, while the difference between the volume at the beginning of the experiment and that after absorption represents the volume of oxygen taken up by the seeds. These relations are expressed by the following formulae, which were used for the calculation:

Let V_r \equiv volume of respirometer,
 V_s \equiv volume of imbibed seeds,
 V_a \equiv volume of absorbent (KOH) used,
 T_1 \equiv initial absolute temperature,
 T_2 \equiv final absolute temperature
 B_1 \equiv initial barometric pressure,
 B_2 \equiv final barometric pressure,
 m_1 \equiv initial manometer reading,
 m_2 \equiv final manometer reading.

$$A: \quad (V_r - V_s) \frac{273}{T_1} \times \frac{B_1}{760}$$

$$B: \quad (V_r - V_s) \frac{273}{T_2} \times \frac{B_1 \pm m_1}{760}$$

$$C: \quad (V_r - V_s - V_a) \frac{273}{T_2} \times \frac{B_2 \pm m_2}{760}$$

Then

$B - C =$ volume of CO_2 eliminated,

$A - C =$ volume of O_2 absorbed.

From these volumes the respiratory quotient (CO_2/O_2) is easily calculated, as are also the milligrams of carbon dioxide eliminated and of oxygen absorbed per gram of imbibed weight per day, using 1.96 mg. as the weight of 1 cc. of CO_2 , and 1.428 mg. as that of 1 cc. of O_2 .²

² The application of these formulae is illustrated in the following calculation of data from an experiment on *Amaranthus*:

$V_r = 24.61$ cc.	$T_1 = 25^\circ \text{C.}$	$B_1 = 751.5$ mm.	$m_1 = -9$ mm.
$V_s = 1.00$ cc.	$T_2 = 25^\circ \text{C.}$	$B_2 = 749.8$ mm.	$m_2 = -65$ mm.
$V_a = 0.76$ cc.			

Weight imbibed seeds = 1.3177 gm.; duration of experiment = 24 hours.

$$\begin{array}{r} 24.61 \\ - 1.00 \\ \hline 23.61 \times \frac{751.5}{760} \times \frac{273}{298} = 21.387 \end{array} \quad (\text{A})$$

$$23.61 \times \frac{740.8}{760} \times \frac{273}{298} = 21.082 \quad (\text{B})$$

$$\begin{array}{r} - 0.76 \\ \hline 22.85 \times \frac{684.8}{760} \times \frac{273}{298} = 18.862 \end{array} \quad (\text{C})$$

$$\text{Log. } \frac{273}{760 \times 298} = 7.081133 - 10$$

log. 23.61 = 1.373096	log. 23.61 = 1.373096	log. 22.85 = 1.358886
log. 751.5 = 2.875929	log. 740.8 = 2.869701	log. 684.8 = 2.835564
- 3.081133	- 3.081133	- 3.081133
<hr/> 1.330158	<hr/> 1.323930	<hr/> 1.275583

Antilog. 1.330158 = 21.387 Antilog. 1.323930 = 21.082 Antilog. 1.275583 = 18.862

$B - C = 21.082 - 18.862 = 2.220$ cc. CO_2 ; $A - C = 21.387 - 18.862 = 2.525$ cc. O_2 ;
 $\text{CO}_2/\text{O}_2 = 0.880$.

log. 2.220 = 0.346353	log. 2.525 = 0.402261
log. 1.96 = 0.292256	log. 1.428 = 0.154728
colog. 1.3177 = 0.880183	colog. 1.3177 = 0.880183
<hr/> 0.518792	<hr/> 0.437172

antilog. 0.518792 = 3.302 mg. CO_2 per gm. imbibed weight per 24 hours.

antilog. 0.437172 = 2.736 mg. O_2 per gm. imbibed weight per 24 hours.

Investigation

The material studied was as follows:

Seeds	Year of crop	Time of collection
<i>Amaranthus retroflexus</i>	1919	August 2–September 7, 1919
<i>Chenopodium album</i>	1918	January 29, 1919
<i>Rumex crispus</i>	1919	August 1919
<i>Crataegus</i>	1917	October 1917

In addition, seeds of *Prunus pumila* (from Mineral Springs, Indiana), and of *P. persica*, *P. armeniaca*, *P. Cerasus* var. *Morella*, *P. domestica* var. Blue Gage, and the red Burbank plum, obtained in the market, were also studied. All rosaceous seeds except *Crataegus* were freed at once from pulp, dried, and in most cases opened and used immediately. *Amaranthus* and *Chenopodium* seeds were stored at room temperature until used. Seeds of *Crataegus* were left at room temperature until they were removed from the carpels, when they were placed at once under germinating conditions at 10° C.

In preparation for an experiment the seeds were placed in distilled water and left in the refrigerator at approximately 10° C. for twenty-four hours. Cotton and filter paper were placed in Petri dishes and the whole sterilized in an electric oven. Before being used, the cotton was saturated with sterile distilled water. The seeds were thoroughly shaken in several portions of sterile water, and were either used at once or placed in the Petri dishes and stored in the refrigerator until needed, in order to avoid the influence on respiration of variations of temperature. By means of these precautions it was possible, to a very great extent, to prevent infection of the seeds with molds or bacteria, and at the same time to avoid the modification of respiration due to treatment with disinfectants (36, 38, 42). The amount of material used depended largely upon the size of the seed and of the apparatus. For *Amaranthus* and *Chenopodium*, 1 gm. of air-dry seeds was the usual amount, a weight representing approximately 1000 seeds. Corresponding numbers and weights for the other seeds were:

Seed	Number	Weight (gm.)
<i>Rumex crispus</i>	0.5
<i>Prunus persica</i>	2	0.7 – 1.00
<i>Prunus domestica</i>	2	0.7 – 0.8
<i>Prunus armeniaca</i>	1	0.8+
<i>Prunus Cerasus</i>	10	0.8
<i>Prunus pumila</i>	10	0.8
<i>Crataegus</i>	50–200	0.7–3.00

With the use of large numbers of seeds, possible in the case of the small seeds of *Amaranthus*, *Chenopodium*, and *Rumex*, individual variations are abolished, and the results are probably more nearly typical than those obtained by the use of one or two seeds, where individual peculiarities would assume an exaggerated significance. From four to ten lots of seeds were run at the same time, since the variability in oxygen consumption and in carbon dioxide elimination was early evident, and it was only by running at least four experiments simultaneously, under precisely similar conditions, that variability could be limited to factors intrinsic in the seed.

The experimental temperature (with rare exceptions) was either 20° C. or 25° C., and the results are all corrected to a comparable basis. The average duration of the experiments was 24 hours. Occasionally a longer time interval was employed, but rarely a shorter, as the amounts of gas absorbed and eliminated were usually small. The average amount of carbon dioxide eliminated during an experiment was 2 cc., with a maximum of 4 cc. The volume of the respirometers was approximately 25 cc. Since KIDD (28) found that 10 per cent of carbon dioxide retards respiration, the accumulation of this gas during an experiment may have slightly modified at times the character of the respiration.

CATALASE DETERMINATION

Table I is a comparison of the catalase activity in the different seeds studied. The variability in catalase activity is extreme,

TABLE I
CATALASE ACTIVITY OF SEED IMMEDIATELY AFTER HARVESTING

SEEDS	WEIGHT OF MATERIAL (GM.)	CONDITION	OXYGEN (CC.) LIBERATED AFTER			
			1 minute	3 minutes	5 minutes	10 minutes
<i>Amaranthus retroflexus</i> .	0.13	Imbibed	3.20	6.10	7.67	8.97
<i>Chenopodium album</i> ...	0.13	Imbibed	3.00	6.05	7.40	7.30
Apricot.....	0.13	Imbibed	10.10	35.10	48.20	56.50
Blue gage plum.....	0.13	Imbibed	7.90	21.40	28.80	35.60
Blue gage plum.....	0.13	As removed from carpel	2.65	9.93	12.68	16.55
Burbank plum.....	0.13	As removed from carpel	2.12	7.85	9.72	11.70
<i>Crataegus</i>	0.0449	As removed from carpel	4.50	10.50	14.30	18.30
<i>Crataegus</i>	0.0688	Imbibed	7.50	18.00	23.10	27.60

especially among the rosaceous seeds. Of these, the greatest activity occurred in apricot, 48 cc. of oxygen being liberated from hydrogen peroxide in five minutes by 0.13 gm. of imbibed seeds. The red Burbank plum had the lowest activity of any rosaceous seed, an equal weight of imbibed seeds liberating only 9.7 cc. of oxygen. In table II the catalase activity of hawthorn is given by periods from the fourth to the forty-second day, while the same

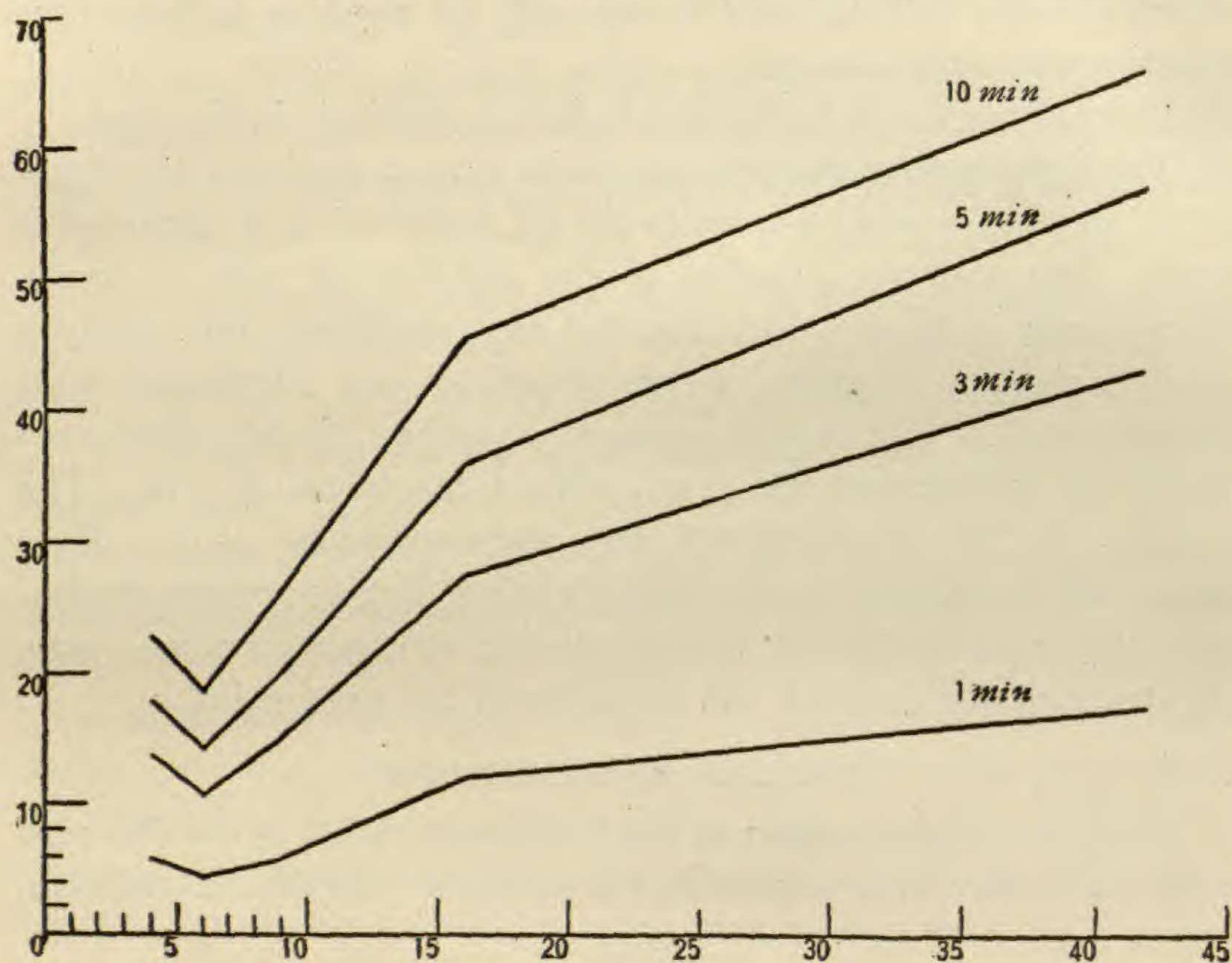


FIG. 1.—Curves of catalase activity at 1, 3, 5, and 10 minute intervals in *Crataegus*: horizontal axes represent time in days after harvesting; vertical axes represent cc. of O₂ liberated; temperature 25° C.

data are presented graphically in fig. 1. There is an increase in catalase activity as after-ripening progresses. A determination made on the after-ripened seeds, 128 days at 10° C., suggests that this increase continues after the forty-second day, but at a very slow rate. This slowness of increase was observed by ECKERSON (19) in her microchemical study of after-ripening in *Crataegus*. The stability of catalase activity in *Amaranthus* during the first month after harvesting is plain from table III.

TABLE II
CATALASE ACTIVITY IN *Crataegus* DURING DORMANCY

NUMBER OF DAYS AT 10° C.	WEIGHT OF MATERIAL (GM.)	OXYGEN (CC.) LIBERATED AFTER			
		1 minute	3 minutes	5 minutes	10 minutes
4.....	0.0410	5.8	13.7	17.9	22.9
6.....	0.0690	4.4	10.6	14.3	18.8
9.....	0.0778	5.7	15.0	20.0	26.2
16.....	0.0773	11.9	27.2	36.0	45.5
42.....	0.0791	17.3	42.9	57.0	65.8
128.....	0.1007	25.6	57.2	65.2*	67.0

*There are two possible explanations for the small increase in catalase activity from the 42nd to the 128th day: (1) the amount of oxygen liberated may have been limited by the use of only 5 cc. of dioxygen; (2) a determination should have been made at 90 days, when after-ripening was complete. After that time the seed may go into a secondary dormancy (18).

TABLE III
CATALASE ACTIVITY IN *Amaranthus retroflexus* (0.13 GM. IMBIBED SEEDS USED)

NUMBER OF DAYS AFTER COLLECTION	OXYGEN (CC.) LIBERATED AFTER			
	1 minute	3 minutes	5 minutes	10 minutes
8.....	3.0	6.2	7.9	9.2
16.....	2.5	5.0	6.2	7.3
28.....	3.4	6.2	7.7	9.0
44.....	3.8	7.2	8.9	10.4

RESPIRATION

Table IV embodies the comparative respiratory behavior of all ten seeds. While all but *Rumex* have a respiratory quotient less than unity, indicating an oxygen intake in excess of the carbon dioxide elimination, the value of the carbon dioxide-oxygen ratio varies within wide limits. For the Rosaceae the “respiratory intensity,” as measured by the milligrams of carbon dioxide eliminated per hour per gram of imbibed seeds, averages about 0.08, while in the other seeds it is higher, being about 0.11 in *Amaranthus*, and 0.15+ in *Rumex* and *Chenopodium*. This difference may be due to the character of the storage substance, chiefly starch (44), present in the last three seeds, but it is undoubtedly also attributable in part to a difference in degree of dormancy.

Only one set of experiments was carried out on *Rumex*, because it was found that even immediately after harvesting the seeds would germinate. In many of the seeds the coats were ruptured and the hypocotyls emerging by the end of the experiment. *Chenopodium* also exhibited a marked readiness to germinate. *Amaranthus* was more dormant, but even within a few weeks of harvesting, on removing the seeds from the respirometer after an experiment, an occasional seed with coat broken was found; while during the later experiments, over 100 days after harvesting, the number with broken coats increased greatly (80 seeds per 1000). The

TABLE IV
RESPIRATORY VALUES (AT 25° C.)

Seeds	No. of experiments	CO ₂ /O ₂	Mg. CO ₂ per 24 hours per gm. imbibed weight	Mg. O ₂ per 24 hours per gm. imbibed weight
<i>Amaranthus retroflexus</i>	37	0.856	2.691	2.324
<i>Chenopodium album</i>	14	0.928	4.213	3.307
<i>Rumex crispus</i>	9	1.160	3.636	2.291
<i>Crataegus</i>	56	0.774	1.548	1.474
Peach.....	14	0.675	1.881	2.033
Apricot.....	30	0.648	2.106	2.392
Cherry.....	19	0.866	2.589	2.186
Sand cherry.....	19	0.876	2.288	1.935
Blue gage plum.....	19	0.696	2.579	2.748
Burbank plum.....	10	0.912	1.998	1.610

rosaceous seeds are really dormant. *Crataegus* requires three months of after-ripening at low temperature (5° C. optimum) before the hypocotyl emerges from the coat. The changes occurring during after-ripening in *Crataegus* progress slowly (19) until very near the end of dormancy. The data reported represent determinations covering the period from the first to the seventy-seventh day under germinating conditions. At this latter time the seeds are still dormant and would fail to germinate if removed to a higher temperature. For the other rosaceous seeds no attempt was made to determine the exact duration of dormancy, although it was observed that seeds left in the refrigerator germinated in from 1.5 to 3 months.

It has been suggested (17) that the dormancy of *Crataegus*, although chiefly conditioned by the embryo, is in part dependent

upon the coats, which reduce the rate of imbibition and perhaps of oxygen entrance. The effect of an atmosphere entirely oxygen was accordingly determined, and it was found that the quotient and the respiratory intensity of the dormant seed still fluctuated. The mean respiratory quotient was a trifle lower than in ordinary air, 0.728 instead of 0.774. Further investigation of this point will determine the effect of varying percentages of oxygen upon the dormant seed and on the after-ripened as well. Although a detailed study of the respiration of the after-ripened seed is yet to be made, data already obtained seem to indicate that the respiratory quotient and the milligrams of carbon dioxide eliminated are

TABLE V

RESPIRATION OF *Amaranthus retroflexus* (AT 25° C.)*

Number of days after harvesting	CO ₂ /O ₂	Mg. CO ₂ per 24 hours per gm. imbibed weight	Mg. O ₂ per 24 hours per gm. imbibed weight
3.....	0.824	2.425	2.150
11.....	0.850	2.263	1.938
24.....	0.892	2.299	1.877
35.....	0.890	2.932	2.417
40.....	0.854	1.955	1.656
71.....	0.877	2.705	2.591
104.....	0.802	4.475	4.056
140.....	0.885	3.979	3.500
176.....	0.842	1.794	1.537

* Seeds stored at room temperature until used.

slightly higher than in the dormant seed, while the oxygen absorption is lower. The effect of increased percentages of oxygen on after-ripened apple seed is to increase its respiratory intensity (25). It may be that this will be found to be the effect on the after-ripened hawthorn.

The values given for *Amaranthus* in table IV are averages based on experiments on seeds at intervals from 3 to 176 days after harvesting. In table V these respiratory values are given by periods, while in fig. 2 the carbon dioxide-oxygen ratio, and the respiratory intensity, as indicated by milligrams of carbon dioxide eliminated as well as of oxygen absorbed, are plotted in a time curve. The uniformity of the carbon dioxide-oxygen ratio is noticeable. The high values for the 104th and 140th days are accompanied by

a slight increase in germination. Still more interesting facts are brought out by the frequency histograms (fig. 3), from which are evident the value most frequently appearing for the carbon dioxide-oxygen ratio, and the total variation of this ratio in the entire number of experiments on each seed. In plotting these histograms the values for the quotients were grouped, and since it was found that experimentally and mathematically the digits for the quotient

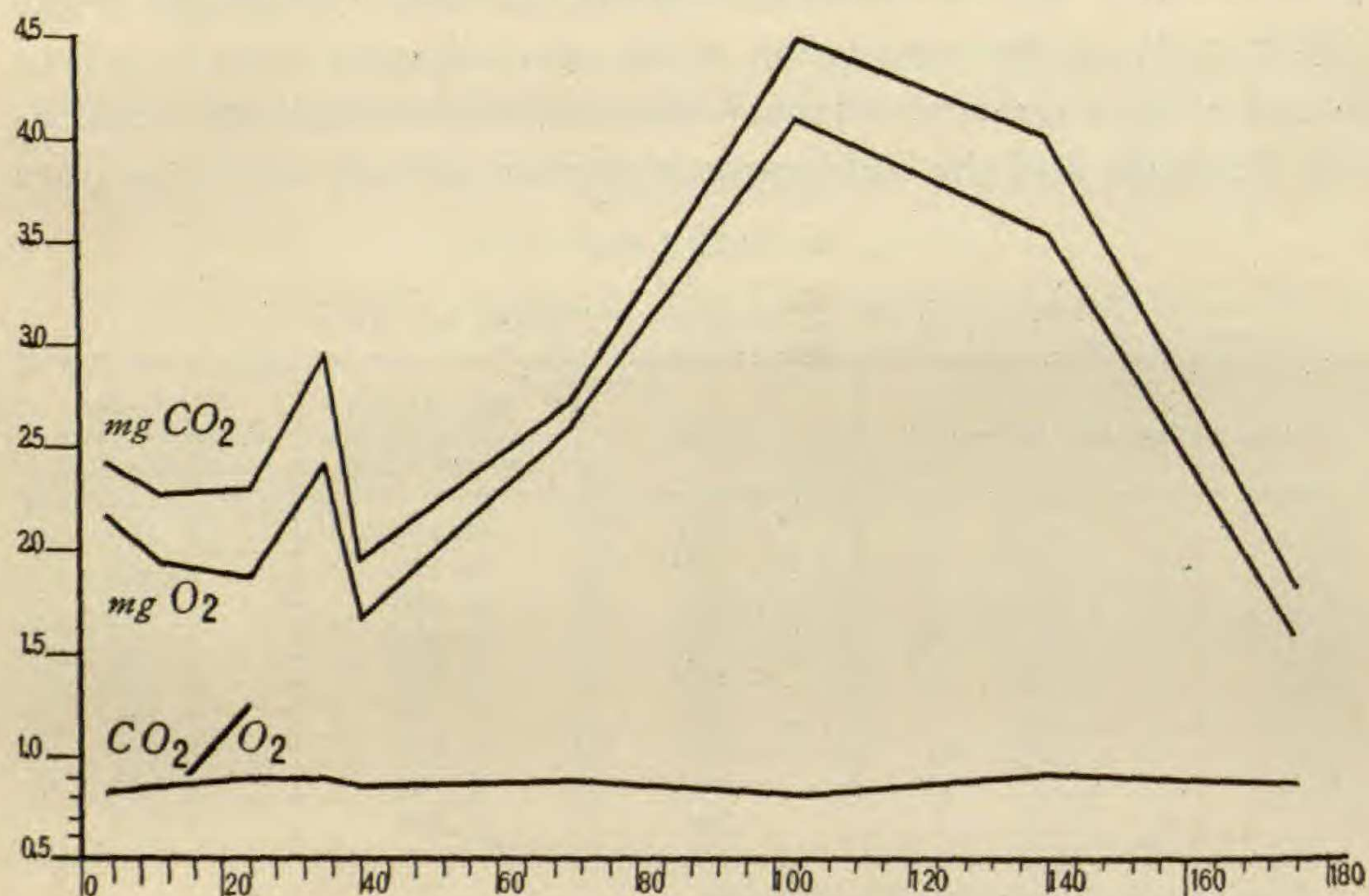


FIG. 2.—Respiration of *Amaranthus retroflexus* under storage at room temperature: horizontal axes represent time in days after harvesting; vertical axes represent values from 0.5 to 4.5 for the CO_2/O_2 , these being absolute numbers indicating ratio; for “respiratory intensity” curves represent mg. of gas per gram imbibed weight of seeds per 24 hours.

are significant only to hundredths, the interval between these groups or classes was taken as 0.01.

The range of the value of this ratio, as determined by the maximum and minimum, varies widely in the different seeds, being least in *Amaranthus* (0.685–0.975, that is, 29 classes) and widest in hawthorn (0.470–1.140, that is, 67 classes). In *Chenopodium* the heaviest grouping lies within a range of only seven classes, but between the lower limit of this group and the next lowest quotient is a gap of nineteen classes, while above the group’s highest limit

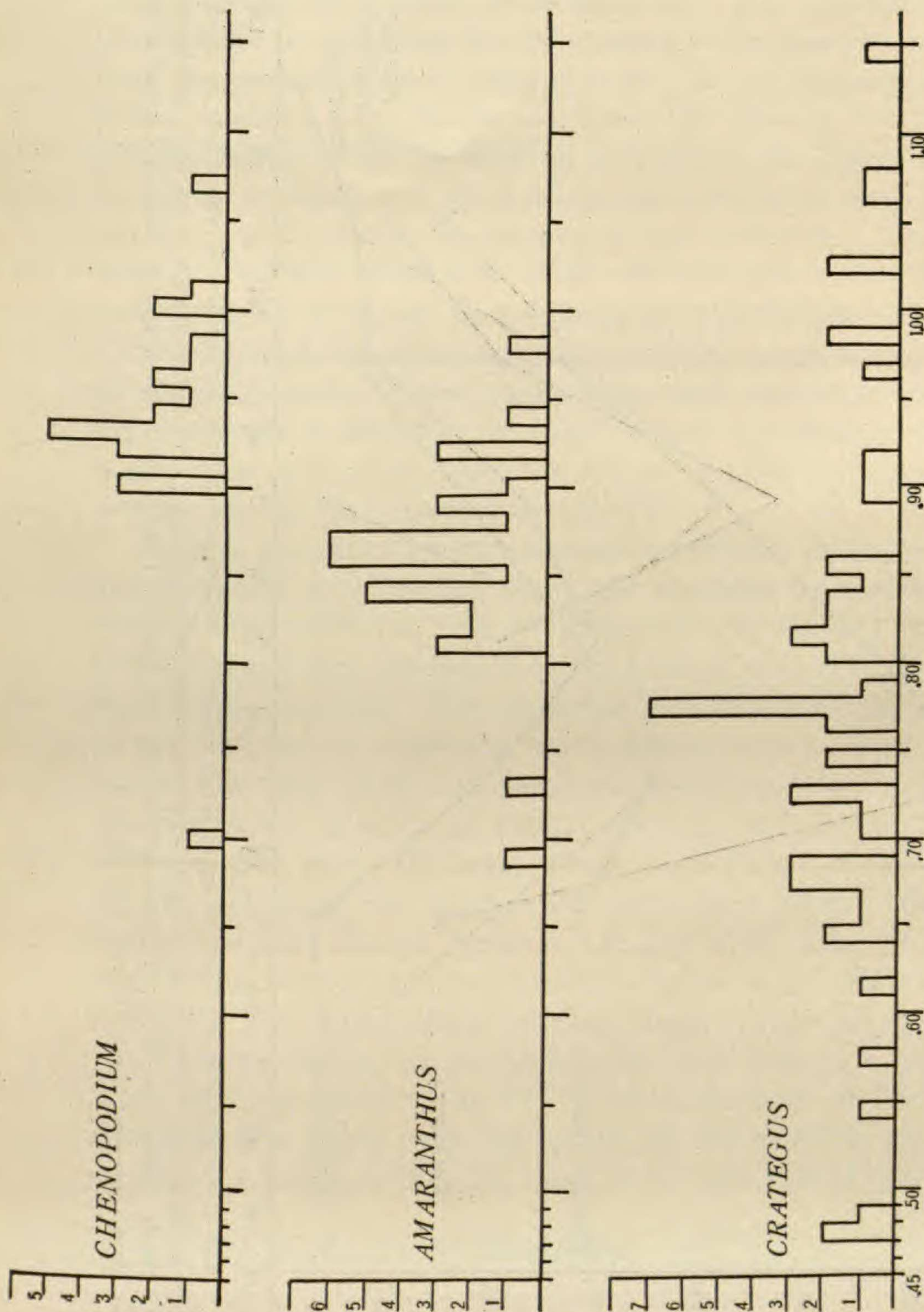


FIG. 3.—Frequency distribution of respiratory quotient in *Crataegus*, *Amaranthus*, and *Chenopodium*: horizontal axes represent class in which respiratory quotients fall; vertical axes represent number of experiments whose quotients fall in given class. Class interval for *Crataegus* 0.01 (0.47-0.48); mean 0.7905; standard deviation 0.079, hence majority of such experiments will tend to vary from 0.79 by 0.08; standard deviation 0.172. Class interval for *Amaranthus* 0.01 (0.685-0.695); mean 0.8578; standard deviation 0.04; standard deviation 0.05. Class interval for *Chenopodium* 0.01 (0.685-0.695); mean 0.9431; standard deviation 0.02; standard deviation 0.04.

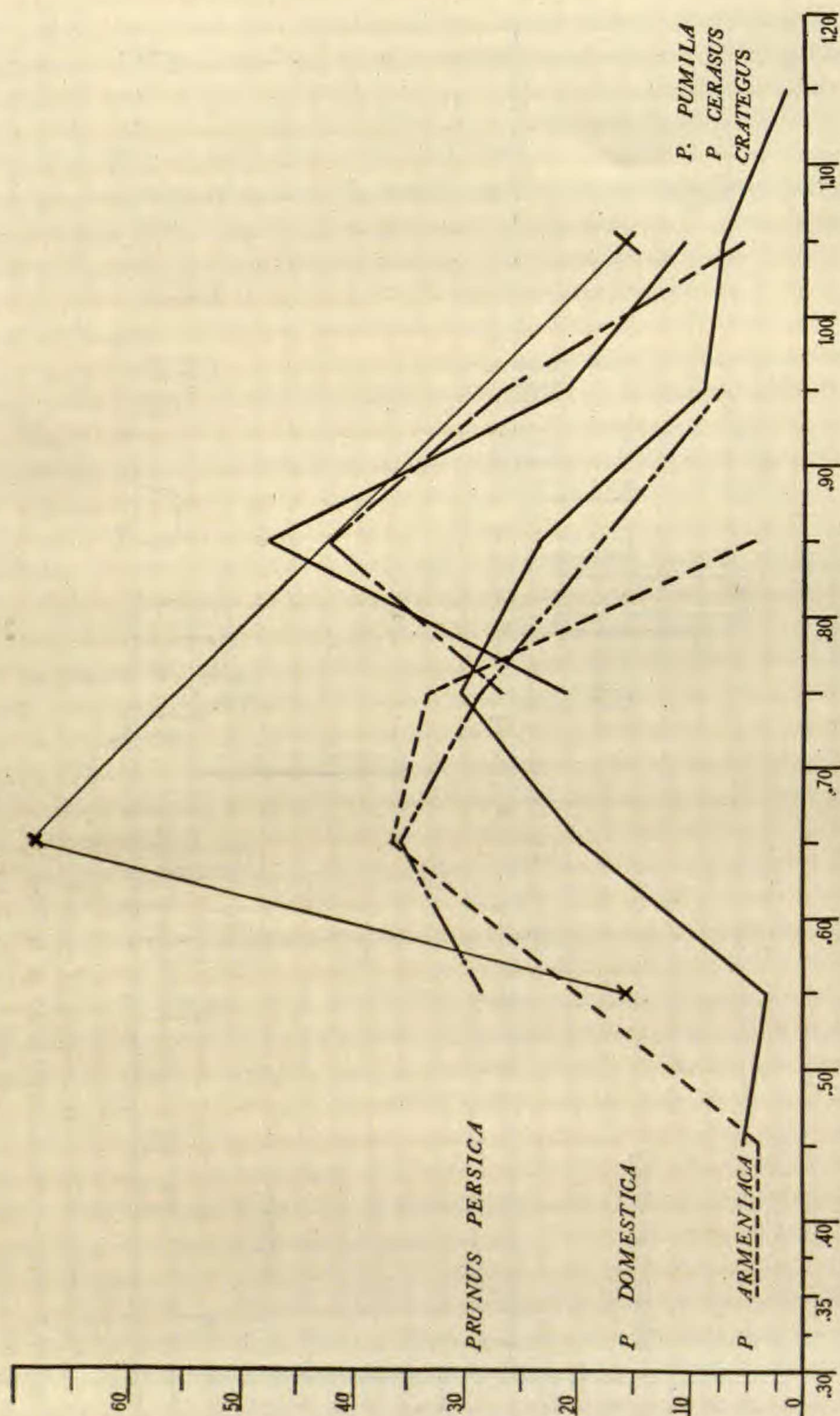


FIG. 4.—Comparison of respiratory quotients in Rosaceae; vertical axes indicate percentages of experiments in which each quotient value occurs; horizontal axes indicate quotient values; grouping is by tenths (from 0.1-0.2, etc.); maximum for peach, apricot, and blue gage plum lies between 0.6 and 0.7 CO₂/O₂ value; for hawthorn between 0.7 and 0.8; for cherry and sand cherry between 0.8 and 0.9.

are five quotients grouped discontinuously. The irregularity and discontinuity of grouping lay the extreme values open to question from the mathematician's point of view. In this instance experimental evidence supports the mathematician's feeling that certain unusual factors must be working to produce the higher values, inasmuch as these were obtained in experiments on seeds of the 1919 crop, tested within two days after their collection. The seeds were not entirely freed from chaff and adherent scales, and in each set mold developed freely during the experiment. The high values obtained, therefore, represent the joint respiratory activity of seeds and mold. These values have been allowed to stand in the histogram to illustrate the value of such treatment of data as a test of its uniformity, but they are not used in calculating the average for the type quotient in table IV.

In fig. 4 the values for the respiratory quotients of the Rosaceae are plotted in a percentage curve, the abscissas representing the value of the quotients, and the ordinates representing the percentage of the total number of experiments on each seed, in which each value occurred. The maximum percentage of the experiments with the six rosaceous seeds, apricot, peach, cherry, sand cherry, blue gage plum, and hawthorn, gives respiratory quotients lying between 0.60 and 0.90, the extreme range of the means for the different seeds (table IV) being twenty-three classes, 0.648–0.876. Within this range the maxima fall into three groups: those of cherry and sand cherry, between 0.80 and 0.90; those of peach, apricot, and blue gage plum, between 0.60 and 0.70; while that of hawthorn lies intermediate between these values (0.70–0.80). Thus the maximum for hawthorn falls very close to 0.756, the mean of the quotients (table IV) for these six seeds; and with the exception of a single value for apricot all the quotients for these rosaceous seeds lie within the range of the quotients of hawthorn.

Discussion

Increase in catalase activity during after-ripening of seeds and during germination has been reported by numerous workers. ECKERSON (19), by microchemical methods, found an increase in the activity of catalase during the after-ripening of *Crataegus*, and

in the present investigation the same phenomenon was observed macroscopically, under after-ripening and germinating conditions. Such an increase during after-ripening is characteristic of seeds with dormant embryos.

On the other hand, in *Amaranthus retroflexus* catalase activity appears to be far less subject to fluctuation. CROCKER and HARRINGTON (16) find surprisingly slight variation in the catalase activity during after-ripening, which in *Amaranthus* occurs "during the first three or four months in dry storage." The activity for the first month and a half after harvesting, as shown in table III, is maintained at a very uniform rate. A comparison of the values obtained on the imbibed seeds with those found by CROCKER and HARRINGTON for the dry powder indicates the uniformity of the degree of activity in different seeds:

WEIGHT OF POWDER (GM.)	OXYGEN (CC.) LIBERATED AFTER		
	1 minute	5 minutes	10 minutes
0.10 dry powder.....	4.9	9.0	11.1
0.13 imbibed seeds...	3.9	6.1	7.1

The values for the dry seeds, however, are slightly higher than for the imbibed, probably owing to the greater concentration of material in a given weight. In this connection the results obtained by CROCKER and HARRINGTON on samples of *Amaranthus* collected in 1894 are of interest. They found the catalase activity of these twenty-three year old seeds but little diminished, although there was complete loss of viability.

DATE OF COLLECTION	OXYGEN (CC.) LIBERATED AFTER			PER CENT GERMINATION AFTER 7 DAYS
	1 minute	5 minutes	10 minutes	
1917 (average of 3 samples).	8.3	20.0	23.8	100
1894 (average of 3 samples).	7.8	17.8	20.8	0

The extreme stability of the catalase activity is emphasized by the fact that one 1894 sample gave values identical with those obtained from one of the 1917 samples:

DATE OF COLLECTION	LOCATION	OXYGEN CC. LIBERATED AFTER			
		1 minute	3 minutes	5 minutes	10 minutes
1917.....	Pullman, Wash.	8.7	18.1	22.7	26.8
1894.....	East Lansing, Mich.	8.7	18.1	22.7	26.8

In the seeds studied in the present investigation, the greatest degree of activity was manifested by the rosaceous seeds (seeds having dormant embryos).

Many plant and animal physiologists have been inclined to postulate a parallelism between catalase activity and respiratory intensity (2, 3, 10, 11, 12, 13). In *Acer saccharum* (27) and *Juniperus virginiana* (38) both catalase activity and respiratory intensity increase as dormancy ends and germination begins. In *Crataegus* catalase activity increased continuously up to the twelfth day in the germinator (the time of the last determination), but the increase was not uniform. Respiratory intensity increased up to the sixth day. From that time to the seventy-seventh day it tended to decrease, but at an irregular rate and with considerable fluctuation. In *Amaranthus* the respiration, like the catalase activity, is maintained at a relatively uniform rate for some time (176 days), but fluctuations in the one are not coincident with fluctuations in the other, and at times may be in an opposite direction. These facts are in harmony with the decision to which their own studies led CROCKER and HARRINGTON, that "in *Amaranthus* seeds there is no evidence of a correlation between catalase activity and respiratory intensity."

That high catalase activity does not necessarily accompany a high respiratory quotient or respiratory intensity (as indicated by milligrams of carbon dioxide eliminated) is evident when the seeds studied are arranged in descending order of these values, as given in table VI.

Although there are relatively few determinations of respiratory values for resting seeds, the literature is rich in findings for other plant parts. A comparison of these values, however, is often difficult because of their variable form and the frequent absence of data necessary for the determination of measured and calculated values.

In table VII results selected from numerous investigations have been recast in such form as to make them comparable with the results on resting seeds obtained in the present study.

In the following discussion of the respiration studies the results are treated as they stand. It is recognized that the temperature at which the experiments were carried out (20° – 25° C.) was high, and undoubtedly led to more vigorous respiration than occurs at 10° C. The transfer from the latter temperature, at which the seeds were stored when under after-ripening or germinating conditions, to the higher temperature of the water bath, may in

TABLE VI

CATALASE ACTIVITY	RESPIRATORY INTENSITY		CO ₂ /O ₂
	Mg. CO ₂ eliminated	Mg. O ₂ absorbed	
1. Apricot.....	Chenopodium	Chenopodium	Rumex
2. Blue gage plum (imbibed) ..	Rumex	Blue gage plum	Chenopodium
3. Crataegus (imbibed).....	Amaranthus	Apricot	Burbank plum
4. Crataegus (as removed from carpels).....	Cherry	Rumex	Sand cherry
5. Amaranthus.....	Blue gage plum	Cherry	Amaranthus
6. Chenopodium.....	Sand cherry	Amaranthus	Cherry
7. Blue gage plum (as removed from carpels).....	Apricot	Peach	Crataegus
8. Burbank plum.....	Burbank plum	Sand cherry	Blue gage plum
9.	Peach	Burbank plum	Peach
10.	Crataegus	Crataegus	Apricot

itself have accelerated respiration. In the case of apple, HARRINGTON (25) finds great diminution of the respiratory intensity at low temperature. An investigation of the respiratory intensity of the seeds used in the present instance for ten degree intervals of temperature will throw light on this point.

The problem of the longevity of seeds is still unsolved, although various theories have been advanced. Loss of vitality might result from exhaustion of stored food, degeneration of enzymes, accumulation in respiration or digestion of substances toxic to the seed, or from still other internal changes in the seed substance inimical to its life. GROVES (14, 23) found that life duration of *Triticum sativum* was a logarithmic function of the temperature, and LEPESCHKIN's time-temperature formula for the coagulation of

TABLE VII

COMPARATIVE RESPIRATION OF DIFFERENT PLANT ORGANS

ORGAN	REF- ERENCE	TEM- PER- ATURE (°C.)	CO ₂ /O ₂	Mg. CO ₂	Mg. O ₂
				Per hour per gm. fresh (or imbibed) weight	
<i>Seedlings</i>					
Triticum.....	5	13	0.98	55.92	41.54
Ricinus communis.....	5	20	0.96	37.67	33.54
Lupinus.....	22	8	1.03	36.49	25.56
<i>Stems of succulents</i>					
Sedum reflexum					
Large stems (day).....	5	31	0.98	23.83	17.70
Large stems (night).....	5	23	0.88	17.05	14.14
Opuntia tomentosa					
Very young (day).....	5	25	0.77	3.86	3.83
Very young (night).....	5	23	0.047	0.412	6.40
<i>Stamens</i>					
Antirrhinum majus					
Anthers.....	32	24	0.87	2.86	5.62
Filaments.....	32	24	1.02	1.32	2.32
Entire.....	32	20	0.93	0.606	0.457
Acanthus mollis					
Adolescent.....	32	21	0.91	1.027	0.806
Young.....	32	21	0.97	0.640	0.482
Adult.....	32	21	0.79	0.538	0.518
Entire.....	32	20	0.81	0.546	0.589
<i>Seeds</i>					
Acer saccharum.....	27	0.27
<i>Petals</i>					
Antirrhinum majus					
Young.....	32	24	1.15	1.613	1.455
Adolescent.....	32	24	1.13	1.374	0.970
Adult.....	32	24	1.00	0.668	0.487
Acanthus mollis					
Young.....	32	26	0.79	1.088	0.952
Adolescent.....	32	26	0.83	0.717	0.606
Adult.....	32	26	0.94	0.633	0.485
<i>Leaves of seedlings</i>					
"Bean" (Phaseolus?).....	22	1.54
Zea Mays					
Green leaves.....	37	26	0.99	1.339	0.979
Etiolated leaves.....	37	26	0.97	1.060	0.795
Vicia Faba					
Green leaves.....	37	21	0.90	1.226	0.988
Etiolated leaves.....	37	21	0.87	0.956	0.794
<i>Leaves of Ligustrum japonicum</i>					
Variegated leaves					
Green parts*.....	37	26	0.84	1.331	1.145
White parts.....	37	26	0.80	1.047	0.958
<i>Germinating seeds</i>					
Phaseolus vulgaris.....	30	1.276
<i>Embryo</i>					
Hordeum vulgare.....	42	24	1.09	1.237

* In a microchemical examination of numerous variegated leaves, ECKERSON found oxidases, peroxidases, and catalases higher in the green than in the white portions.

TABLE VII—Continued

ORGAN	REF- ERENCE	TEM- PER- ATURE (°C.)	CO ₂ /O ₂	Mg. CO ₂	Mg. O ₂
				Per hour per gm. fresh (or imbibed) weight	
<i>Pistils</i>					
Antirrhinum majus, entire.....	32	20	1.00	1.186	0.864
Acanthus mollis					
Young.....	32	21	0.89	0.609	0.492
Adolescent.....	32	21	0.87	0.531	0.428
Entire.....	32	20	0.84	0.490	0.409
Adult.....	32	21	0.90	0.486	0.387
<i>Germinating seeds</i>					
Lupinus albus.....	30	0.990
Vicia Faba.....	30	0.970
Pisum sativum.....	30	0.946
Cucurbita Pepo.....	30	0.878
<i>Flowers</i>					
Syringa vulgaris.....	22	20	0.788
<i>Leaves and leaflike structures</i>					
Sepals of Acanthus mollis					
Adolescent.....	23	24	1.03	0.798	0.565
Young.....	33	24	1.06	0.562	0.858
Adult.....	33	24	0.88	0.554	0.444
<i>Leaves</i>					
Triticum sativum seedling					
Green.....	37	25	0.97	0.788	0.588
Etiolated.....	37	25	0.98	0.735	0.431
Hordeum vulgare seedling					
Green.....	37	23	0.85	0.521	0.444
Etiolated.....	37	23	0.83	0.423	0.371
Acanthus mollis.....	37	22	0.77	0.361	0.212
Antirrhinum majus.....	37	24	0.73	0.354	0.182
Antirrhinum majus.....	37	22	0.88	0.314	0.251
Malva sylvestris.....	37	15	0.71	0.251	0.246
Syringa vulgaris.....	9	22	0.94
Syringa vulgaris.....	33	22	0.94
Taxus baccata.....	9	16	0.86
Pinus maritima.....	9	20	0.85
Pinus sylvestris.....	9	24	0.80
Eucalyptus.....	9	19	0.80
<i>Leaf blades</i>					
Vicia sativa.....	37	18	0.75	0.590	0.574
Rumex pulcher.....	37	17	0.76	0.288	0.276
Geranium Robertianum.....	37	18	0.72	0.272	0.275
Bryonia dioica.....	37	17.5	0.65	0.259	0.290
<i>Leaf petioles</i>					
Vicia sativa.....	37	18	0.88	0.327	0.207
Bryonia dioica.....	37	17.5	0.87	0.184	0.154
Geranium Robertianum.....	37	18	0.91	0.086	0.068
Rumex pulcher.....	37	17	0.80	0.064	0.058
<i>Tendrils</i>					
Vicia sativa.....	37	18	0.90	0.504	0.408
Bryonia dioica.....	37	17.5	1.02	0.221	0.157
<i>Cladodes</i>					
Asparagus albus.....	37	18	0.78	0.437	0.410
Ruscus hypophyllum.....	37	15	0.55	0.051	0.067

TABLE VII—Continued

ORGAN	REF- ERENCE	TEM- PER- ATURE (°C.)°	CO ₂ /O ₂	Mg. CO ₂	Mg. O ₂
				Per hour per gm. fresh (or imbibed) weight	
Phyllodes					
Acacia megaloxylon.....	37	18	0.66	0.233	0.257
Entire plant					
Pelargonium zonale.....	22	12-14	0.54
Sedum hybridum.....	22	25-26	0.37
Buds					
Aesculus					
Influence of warm bath.....	35	20	0.188
14 hours in water at 38° C.....	35	20	0.138
14 hours in water at 20° C.....	35	20	0.122
Stems					
Vicia sativa.....	37	18	0.86	0.292	0.247
Rumex pulcher.....	37	17	0.85	0.231	0.197
Asparagus albus.....	37	18	0.96	0.221	0.167
Accacia megaloxylon.....	37	18	0.82	0.206	0.182
Bryonia dioica.....	37	17.5	0.91	0.167	0.133
Geranium Robertianum.....	37	18	0.94	0.127	0.097
Mesembryanthemum nodiflorum.....	37	15.5	1.00	0.076	0.055
Ruscus hypophyllum.....	37	15	0.58	0.033	0.414
Bulbs					
Convallaria					
Untreated.....	35	19	0.174
After 8 hours in water at 38° C....	35	19	0.133
After 8 hours in water at 18° C....	35	19	0.117
Imbibed seeds					
Juniperus					
130 days at 5° C.....	38	25	0.95	0.489	0.4398
100 days at 5° C.....	38	25	0.68	0.2486	0.3192
90 days at 5° C.....	38	25	0.97	0.2354	0.2092
60 days at 5° C.....	38	25	0.97	0.2352	0.2152
30 days at 5° C.....	38	25	0.94	0.218	0.1976
5 days at 5° C.....	38	25	0.84	0.1311	0.1347
Table					
Chenopodium album.....	IV	20	0.928	0.175	0.141
Rumex crispus.....	"	20	1.16	0.151	0.095
Amaranthus retroflexus.....	"	20	0.857	0.113	0.096
Prunus cerasus var. Morello.....	"	20	0.814	0.108	0.091
P. domestica (blue gage).....	"	20	0.695	0.107	0.109
P. pumila.....	"	20	0.878	0.093	0.076
P. armeniaca.....	"	20	0.628	0.089	0.102
P. domestica (Burbank plum).....	"	20	0.912	0.083	0.067
P. persica.....	"	20	0.675	0.078	0.084
Crataegus.....	"	20	0.774	0.064	0.061
Zea Mays					
Embryo.....	42	20	0.83	0.444
Endosperm.....	42	21	0.55	0.014
Aleurone.....	42	0.009
Pure endosperm.....	42	22	0.73	0.004
Intact seed.....	42	18	0.77	0.003
Hordeum vulgare					
Intact seed.....	42	26	0.83	0.203
Endosperm (summer).....	42	23	0.68	0.078
Aleurone (summer).....	42	0.052
Endosperm (winter).....	42	15	0.58	0.019

TABLE VII—*Concluded*

ORGAN	REF- ERENCE	TEM- PER- ATURE (°C.)	CO ₂ /O ₂	Mg. CO ₂ Mg. O ₂	
				Per hour per gm. fresh (or imbibed) weight	
Pure endosperm (summer).....	42	23	0.36	0.019
Pure endosperm (winter).....	42	20	0.39	0.007
Aleurone (winter).....	42	0.001
Ricinus.....	42	18	0.59	0.082
<i>Tubers</i>					
<i>Solanum</i>					
Entire.....	22	0.006
5 hours after quartering.....	22	0.480†
Untreated.....	35	17-19	0.013
After 6 hours in water at 19.5° C.	0.010
After 5 hours in water at 40° C....	35	0.018
After storage at 0° C. (starch changed to sugar).....	35	19	0.059
After 8 hours 2 per cent aqueous ether.....	35	19	0.068
<i>Fruits</i>					
Russet apple.....	21	18	1.09	0.019	0.014
Orange.....	21	18	1.06	0.078	0.164
Japanese plum.....	21	18	1.30	0.274	0.160
<i>Dry seeds</i>					
<i>Triticum vulgare</i>					
19 per cent water.....	43	0.0054
Soft red winter wheat (13 per cent water).....	6	0.00024
<i>Secale cereale</i>					
19 per cent water.....	43	0.0001
<i>Zea Mays</i>					
19 per cent water.....	43	0.0001
<i>Juniperus dry seeds</i>	38	25	0.76	0.00098	0.0011
<i>Hordeum distichum</i>					
33 per cent water.....	29	0.0001
19-20 per cent water.....	29	0.00015
15 per cent water.....	29	0.00004
<i>Algae</i>					
<i>Nostoc</i>	9	19	0.40
<i>Fucus</i>	9	14-15	0.50
<i>Fungi</i>					
<i>Aspergillus niger</i> , Raulin's solution					
Vegetative mycelium (morning)...	39	1.04+
Vegetative mycelium (evening)...	39	1.05
Fruiting mycelium (evening).....	39	1.07
Water and 0.4 per cent salts, black conidia.....	39	23.5	0.66
<i>Sterigmatocystis nigra</i>					
In solutions containing					
2 gm. tannin.....	21	1.09
0.9 gm. sugar.....	21	20	0.93
0.984 gm. tartaric acid.....	21	1.78
0.75 gm. citric anhydride.....	21	33	1.40
0.88 gm. malic acid.....	21	20	1.50
0.80 gm. citric acid.....	21	20	1.48

† Cf. MAGNESS (31): "Removal of the epidermis facilitates the entrance of oxygen to the tissues and escape of carbon dioxide. It would be interesting to know to what extent the increased respiration following wounding is due to mechanically facilitating gaseous exchange and to what extent it is due to actual metabolic changes in the wounded tissues."

proteins was applicable as a temperature-life duration formula for wheat grains, as LEFESCHKIN himself had found it applicable for imbibed cells. Loss of viability in air-dry seeds, therefore, is probably due to "a time-temperature denaturing of certain colloids (probably proteins) of the embryo" (16). The retarding effect of carbon dioxide upon germination has been shown by KIDD (28). On the other hand, enzymes may persist and have a high degree of activity in seeds which are no longer viable, as in *Amaranthus*, or their activity may be greatly decreased without marked decrease in percentage of germination, as in Johnson and Sudan grasses (CROCKER 16). Exhaustion of stored food cannot be considered a cause for decreased life duration in air-dry seeds, but in the case of seeds lying in the soil the situation is different. Such seeds would have a high water content, favoring chemical action, whether respiration or digestion. The actual occurrence of such reactions of course would depend upon oxygen supply, temperature, enzymes present, and the extent to which by-products (carbon dioxide, etc.) were removed. In such seeds, of which *Amaranthus* is a typical example, the life duration might easily be limited by the amount of stored substance present or by the rapidity with which it was respired or digested.

CROCKER and HARRINGTON (16), in studying the behavior of Johnson grass, found that storage of freshly harvested seed at 20° C. in the germinator led to an increased or secondary dormancy, a phenomenon frequently observed in seeds as a result of unfavorable germinating conditions. They suggest that such a deepened dormancy, if accompanied by a decreased respiration, may have an important bearing upon the longevity of seeds in the soil by lengthening the period necessary for the reduction of stored foods. From their own experiments on the respiration of Johnson grass they estimate the possible longevity of this seed as follows:

If 75 per cent of the weight of the seed can be respired before death occurs, secondarily dormant Johnson grass seeds could lie in a germinator for 9.8 years at 20° C. before death would occur from exhaustion of stored foods. The period at 10° C. would likely be 2 to 3 times 9.8 years, in accord with the temperature quotient for respiration. Without such a reduction in respiratory intensity the possible longevity would be a little more than one-third as great, figured on the initial rate in the active seeds. Even if the longevity of imbibed seeds in the soil be dependent upon some contingent other than

exhaustion of stored food, this reduction in respiration is of significance. It will leave more stored material for building purposes in case germination does occur after a considerable period in the soil.

A similar calculation has been made of the rapidity with which *Amaranthus* seeds respiring at the rate observed (table IV) would exhaust their storage substance. The estimate is based on a moisture content of 47.43 per cent, and Woo's (44) analysis showing 47 per cent starch. On this basis the possible longevity is 160 days at the experimental temperature, 20°–25° C. This temperature is high, and respiration of stored food would certainly proceed more slowly at the lower temperature of the soil. Moreover, since observation (7, 8, 24, 41) shows the actual longevity of *Amaranthus* in the soil to be more than thirty years, there must be tremendous curtailment of metabolism under these conditions, with exceedingly slow use of the reserve. Even in the laboratory, dry-stored at room temperature and imbibed just before using, the seeds were viable 176 days after harvesting, and CROCKER reports that 200 days in the germinator at 20° C. does not alter their viability. If the 47 per cent fat contained in hawthorn be taken as stearin, the longevity of this seed when removed from the carpel, with 60 per cent water content, would be about 170 days at the rate of respiration observed (table IV) for the same temperature. Actually the seeds are viable for a longer time.

In all the rosaceous seeds studied variability of respiratory values was marked. Since the value of the respiratory quotient is based upon the volumes of CO₂ eliminated and of O₂ absorbed, it may serve as a convenient index of this variability. The total range of the quotient values of the six rosaceous seeds is 0.31–1.14. The extremes for individual seeds are as follows:

Hawthorn	0.47–1.14
Peach	0.56–0.96
Apricot	0.31–0.80
Cherry	0.76–1.04
Sand cherry	0.75–1.05
Blue gage plum	0.57–1.02
Burbank plum	0.72–1.04

As shown in fig. 4, with the exception of a single experiment on apricot, the quotients for all the other rosaceous seeds fall within the range of those of hawthorn. The mean for hawthorn (0.774)

lies within 0.02 of the mean of the means (table IV) for the other seeds (0.756). The rosaceous seeds, therefore, exhibit a marked similarity to one another in their respiratory behavior. If it may safely be assumed, as has been the tendency, especially among animal physiologists, that the character of respiration and particularly of the respiratory quotient depends upon the kind of substance oxidized, such a similarity would be expected, since in all these seeds the storage substance is chiefly fat.

On the other hand, in *Amaranthus*, although fluctuations in the carbon dioxide elimination and the oxygen absorption occur, and that too not always in the same, but occasionally in opposing, directions, the respiratory quotient remains relatively stable throughout a period of 176 days. The contrast in the behavior of the Rosaceae and of *Amaranthus* may be due in part to the difference in storage material, since *Amaranthus* contains little fatty substance (44), but much starch. This latter substance constitutes the reserve in *Chenopodium* and in *Rumex* also. It is probable, however, that other factors are responsible for the extreme variability of the rosaceous quotients.

The embryo of *Amaranthus* is not dormant. "Any time after maturity naked embryos are capable of immediate growth" (16). The six rosaceous seeds have dormant embryos. This dormancy, however, is of unequal intensity in different parts of the embryo. DAVIS and ROSE (17) and ECKERSON (19) have emphasized the difference in development of cotyledons and of the hypocotyl in *Crataegus*. DAVIS (18) finds a similar situation in the peach. It is therefore reasonable to suppose that these two parts of the embryo, cotyledons and hypocotyl, differing as they do physiologically and chemically, may differ in their metabolic activity and specifically in their oxygen absorption and carbon dioxide elimination. These differences at times may counterbalance, or at times augment, each other; or it may be that now the intensity of the hypocotyl, now that of the cotyledons, may predominate and determine the metabolism characteristic of the seed as a whole.

An analogous situation is reported by MAIGE (32) for stamens. In general the respiratory intensity of the adult stamen is less than that of the young organ, but this decreased intensity is differently attained in different plants. In some there is a steady decrease

from youth to age, while in others there may be an increase to a maximum followed by decline to the adult intensity, or a fall to a minimum succeeded by a return to a rate slightly lower than that at the beginning. Study of the filament and anther separately reveals the fact that their respiratory intensities are distinctly different, the anther undergoing a sort of grand period of respiratory intensity, while the intensity of the filament increases regularly from immaturity to maturity. The intensity of respiration of the stamen as a whole therefore is the resultant between these two respiratory intensities.

Great diversity of opinion exists as to the importance attaching to the respiratory quotient as an index of metabolism. In seeds like *Amaranthus* and *Chenopodium* the quotient would appear to be of significance because of its stability. The variability of the quotient in Rosaceae at first might appear to militate against its possessing any significance. When, however, this variability of the quotient is found to characterize a group possessing fundamental physiological and chemical features in common, it would seem that even here some significance might attach to the quotient. It may be of little value as indicating the material oxidized, but it may have considerable importance as indicating a situation due to the interplay of several factors. The quotient percentage curves (fig. 4) and the frequency histograms (fig. 3) show more clearly than do the tabulated data the general trend of respiration. From them can be seen that even with their variability the values for hawthorn and the other Rosaceae tend to fall into small groups about one largest assemblage. The latter, therefore, may be considered indicative of the type respiratory value for the seed.

In *Chenopodium* and *Amaranthus* the massing of the quotients is within a narrow range, and the type is more marked. Treatment of data in this way, therefore, may serve as a further check on the uniformity of conditions under which the experiments are carried out, and perhaps on the reliability of the method.

In this connection it is interesting to note that the curves in fig. 3 are of the kind found by PEARSON to be typical for botanical measurements, limited skew curves ("axis of the abscissas limited

on both sides, curve unsymmetrical"). Zoological curves, on the contrary, are unlimited skew curves ("axis of abscissas unlimited on both sides, curve unsymmetrical," 45). A possible explanation of this difference in behavior between plants and animals that suggests itself is the complication of the results of zoological experimentation due to the independent volition of the animal. Plants, placed under a given set of conditions, vary little in behavior, while uniformity of behavior in the case of different animals, or even in the case of the same animal upon successive occasions, is beyond control.

These respiratory studies in no wise answer the queries that they suggest. They are rather preliminary to further investigation. Upon one point, the difference in respiration between dormant and after-ripened but still resting *Crataegus* seeds, some data have already been obtained. That the respiration is slightly higher in the after-ripened than in the dormant seed seems well established. Further study of this point, however, is necessary.

Summary

1. The respiratory intensity, that is, the mg. CO₂ eliminated per gram imbibed seeds per hour, was determined experimentally for *Amaranthus retroflexus*, *Chenopodium album*, and *Rumex crispus*, as well as for *Crataegus* and certain drupaceous Rosaceae. Determinations of the catalase activity were also made for most of the seeds.

2. Catalase activity increases in *Crataegus* under after-ripening and germinating conditions (10° C.), up to the forty-second day. The slightly higher value for the 128th day may represent: (1) a continued increase at an extremely slow rate; (2) a limit depending on the amount of dioxogen used (5 cc.); (3) a falling off, as a result of secondary dormancy, of an activity whose maximum occurred at the completion of after-ripening (about the ninetieth day). Respiration reaches a maximum intensity much earlier (sixth to eighth day), and thereafter exhibits a slow and fluctuating decline, at least to the seventy-seventh day.

3. In *Amaranthus* both catalase activity and respiration are relatively stable. Fluctuations in catalase activity and in respiratory

intensity do not occur simultaneously, and may be in opposite directions.

4. The respiratory quotient and respiratory intensity vary markedly for different seeds, and in the Rosaceae for different lots of the same kind of seed under precisely similar experimental conditions. The respiratory quotient in *Amaranthus* and *Chenopodium* is markedly stable. Since in the Rosaceae the embryo is dormant, while in the other two seeds it is not, it may be that this difference in behavior is characteristic of seeds with dormant embryos, and the greater stability of respiration in *Amaranthus* and in *Chenopodium* represents the attainment of a more stable metabolism in these seeds.

5. Stability or variability of the quotient may be of significance as indicative of the possibility of an interplay of several factors on the metabolism. In *Crataegus*, and presumably in the other Rosaceae, the marked variability is probably the resultant between the respiration of the dormant hypocotyl and that of the mature cotyledons.

6. The arrangement of the respiratory quotients for each seed in a curve showing the percentages of the experiments with each seed giving each value, and in frequency histograms in which are plotted the actual number of experiments in which each quotient value occurred, indicates the tendency of each seed toward a typical respiration. The quotients for *Chenopodium* and *Amaranthus* are 0.928 and 0.856 respectively, while those of the Rosaceae form three groups within a range of 0.118. In the first group, between 0.648 and 0.7, fall the quotients for apricot, peach, and blue gage plum; in the third, between 0.8 and 0.876, those of cherry and sand-cherry; while that of hawthorn, 0.774, lies midway between.

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LITERATURE CITED

1. APPLEMAN, C. O., Some observations on catalase. BOT. GAZ. 52:182-192. 1911.
2. ———, Relation of catalase and oxidase to respiration in plants. Md. Agric. Expt. Sta. Bull. 191. 1915.
3. ———, Respiration and catalase activity in sweet corn. Amer. Jour. Bot. 5:207-209. 1918.
4. ATWOOD, W. M., A physiological study of the germination of *Avena fatua*. BOT. GAZ. 57:386-414. 1914.
5. AUBERT, E., Recherches sur la respiration et l'assimilation des plantes grasses. Rev. Gén. Botanique 4:203-219, 273-282, 320-331, 337-353, 373-391, 421-441, 497-502, 558-568. 1892.
6. BAILEY, C. H., and GURJAR, A.M., Respiration of stored wheat. Jour. Agric. Res. 12:685-713. 1918.
7. BEALE, W.J., The vitality of seeds buried in the soil. Mich. Agric. Exper. Sta. Bull. 5. 1885.
8. ———, Vitality of seeds buried in the soil. Proc. 31st Ann. Meeting Soc. Prom. Sci. 1910.
9. BONNIER, G., and MANGIN, L., Recherches sur la respiration des feuilles à l'obscurité. Ann. Sci. Nat. Bot. VI. 19:216-255. 1884.
10. BURGE, W. E., Relation between the amount of catalase in the different muscles of the body and the amount of work done by these muscles. Amer. Jour. Physiology 41:153-161. 1916.
11. ———, A comparison of the amount of catalase in the muscles of active and inactive animals. *Ibid.* 42:600. 1916-1917.
12. ———, Comparison of the catalase content of the breast muscle of wild pigeons and of bantam chickens. Science N.S. 46:440. 1917.
13. ———, Catalase content of luminous and non-luminous insects compared. *Ibid.* 46:295. 1917.
14. CROCKER, WM., Mechanics of dormancy in seeds. Amer. Jour. Bot. 3:99-120. 1916.
15. CROCKER, WM., and DAVIS, W. E., Delayed germination in *Alisma Plantago*. BOT. GAZ. 58:285-321. 1914.
16. CROCKER, WM., and HARRINGTON, G. T., Catalase and oxidase content of seeds in relation to their dormancy, age, vitality, and respiration. Jour. Agric. Res. 15:137-174. 1918.
17. DAVIS, W. E., and ROSE, R. C., The effect of external conditions upon the after-ripening of the seeds of *Crataegus mollis*. BOT. GAZ. 54:49-62. 1912.
18. DAVIS, W. E., Unpublished work on the peach.
19. ECKERSON, S. H., A physiological and chemical study of after-ripening. BOT. GAZ. 55:286-299. 1913.
20. GARREAU, ———, De la respiration chez les plantes. Ann. Sci. Nat. Bot. III. 15:1-36. 1851.
21. GERBER, C., Recherches sur la maturation des fruits charnus. Ann. Sci. Nat. Bot. VIII. 4:1-277. 1896.
22. GRAFE, V., Ernährungsphysiologisches Praktikum höherer Pflanzen. 1914.

23. GROVES, J. F., Temperature and life duration of seeds. BOT. GAZ. 63: 169-189. 1917.
24. HARRINGTON, G. T., Agricultural value of impermeable seeds. Jour. Agric. Res. 6:761-796. 1916.
25. ———, Unpublished work on the apple.
26. HARRINGTON, G. T., and CROCKER, WM., Respiration measurements (unpublished).
27. JONES, H. A., Physiological study of maple seeds. BOT. GAZ. 69:127-152. 1920.
28. KIDD, F., The controlling influence of carbon dioxide in the maturation, dormancy, and germination of seeds. Proc. Roy. Soc. Lond. B. 87:408-421, 609-623. 1914; 89:136-156. 1916.
29. KOLKWITZ, R., Über die Athmung ruhender Samen. Ber. Deutsch. Bot. Gesells. 19:285-287. 1901.
30. LEWIN, M., Über die Atmung keimender Samen unter Druck. Ber. Deutsch. Bot. Gesells. 23:100-104. 1905.
31. MAGNESS, J. R., Composition of gases in intercellular spaces of apples and potatoes. BOT. GAZ. 70:308-316. 1920.
32. MAIGE, MME., Recherches sur la respiration de l'étamine et du pistil. Rev. Gén. Botanique 21:32-38. 1909.
33. ———, Recherches sur la respiration des différents pièces florales. Ann. Sci. Nat. Bot. IX. 14:1-62. 1911.
34. MAQUENNE, L., Sur le mécanisme de la respiration végétale. Compt. Rend. 119:697-699. 1894.
35. MÜLLER-THURGAU, H., and SCHNEIDER-ORELLI, O., Beiträge zur Kenntnis der Lebensvorgänge in ruhenden Pflanzenteilen. I. Flora. 101:309-372. 1910; II. Ibid. 104:385-441. 1911-1912.
36. NABOKICH, A. J., Über den Einfluss der Sterilization der Samen auf die Atmung. Ber. Deutsch. Bot. Gesells. 21:279-291. 1903.
37. NICOLAS, G., Recherches sur la respiration des organes végétatif des plantes vasculaires. Ann. Sci. Nat. Bot. IX. 10:1-113. 1909.
38. PACK, D. A., After-ripening and germination of *Juniperus communis*. BOT. GAZ. 71:32-60. 1920.
39. PURIEWITSCH, K., Physiologische Untersuchungen über Pflanzenathmung. Jahrb. Wiss. Bot. 35:573-610. 1900.
40. ROSE, R. C., After-ripening and germination of seeds of *Tilia*, *Sambucus*, and *Rubus*. BOT. GAZ. 67:281-308. 1919.
41. SHULL, G. H., The longevity of submerged seeds. Plant World 17:329-337. 1914.
42. STOWARD, F., On endospermic respiration in certain seeds. Ann. Botany 22:415-648. 1908.
43. WHITE, J., Ferments and the latent life of resting seeds. Proc. Roy. Soc. Lond. B. 81:417-442. 1909.
44. WOO, M. L., Chemical constituents of *Amaranthus retroflexus*. BOT. GAZ. 68:313-344. 1919.
45. ZIZEK, F., Statistical averages. 1913.